REPRODUCTIVE CORRELATES OF ENVIRONMENTAL VARIATION AND NICHE EXPANSION IN THE CAVE SWALLOW IN TEXAS

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Natural and anthropogenic environmental factors interact to form the selective background that shapes the reproductive variability of many avian species. An excellent subject for investigations of such interactions is the Cave Swallow (*Petrochelidon fulva*), a relatively widespread cavern-nesting species presently undergoing human-mediated breakdown of ecological segregation from other swallows at the northeastern periphery of its range in North America. Martin (1974, 1980), Martin and Selander (1975), and Martin and Martin (1978) have discussed range expansion and intergeneric hybridization as consequences of highway culvert nesting in this species, while Martin et al. (1977) outlined the basic pattern of reproduction of a cavern-nesting colony. At the cavern site, minimal or nonexistent nest predation and interspecific competition, little human disturbance, constant availability of nesting material and minimal temperature fluctuation operate together to increase environmental stability, and enhance the value of correlations between patterns of reproduction and the few environmental factors that do fluctuate here. Such diminished ecological variability resembles that characteristic of islands (MacArthur and Wilson 1967; Cody 1966, 1971) and suggests comparisons of the reproductive parameters of cavern populations of *P. fulva* with those of culvert colonies exposed to more variable selective influences. In this report, I (1) document variation in reproduction in an isolated cave colony of *P. fulva* in successive years; (2) use these data to test the general hypothesis that directly relates reproductive output and success to amount of precipitation in xeric areas; and (3) contrast reproductive patterns of cave and culvert populations of this species and discuss possible reasons for their disparity.

STUDY AREA AND METHODS

During 1974 and 1975, data were taken at an isolated colony of Cave Swallows nesting at Dunbar Cave, 37 km WSW Rocksprings, Edwards Co., Texas. Additionally in 1974, Cave Swallow colonies that nested syntopically with Barn Swallows (*Hirundo rustica*) in four highway culverts were visited; these were located in Kinney and Uvalde counties, approximately 73 km SE of the cave site, along 23 km of U.S. Highway 90 beginning at and extending eastward from 13 km E of Brackettville. All sites lie just east of the Chihuahuan Desert in a region of gently rolling, sparsely vegetated hills dissected by semi-permanent and temporary streams.

TABLE 1
STUDY AREA PRECIPITATION (1974 AND 1975) IN CM PRECEDING AND DURING FIRST AND SECOND REPRODUCTIVE CYCLES OF CAVE SWALLOWS[1]

| | Precipitation | | | |
| | 1974 (Dry) | | 1975 (Wet) | |
Location	Jan.–May[2]	Jan.–July[3]	Jan.–May	Jan.–July
Carta Valley (13 km W cave)	13.20	16.70	22.89	44.39
Rocksprings (40 km NW cave)	17.45	20.40	36.58	55.65
Brackettville (59 km SSE cave)	15.11	16.64	29.85	51.79

[1] Data from NOAA 1974, 1975, 1976.
[2] Period precedes and includes first reproductive cycle of season.
[3] Period precedes and includes first and second reproductive cycles.

Precipitation and temperature data (NOAA 1973, 1974, 1975) from Carta Valley (29°48′N, 100°48′W), 13 km W of Dunbar Cave, and from Brackettville (29°19′N, 100°24′W) were considered representative of those at cave and culvert sites, respectively; Table 1 presents rainfall data for these and for other reference sites in the cave area. Ambient temperatures at representative nest-sites were monitored with recording thermographs.

Dunbar Cave opens by a vertical shaft approximately 2.3 m in diameter and 3.4 m in length into the roof of a chamber nearly 25 m in greatest diameter and 5 m in height. Here, a colony of from 250–300 pairs of *P. fulva* nested in isolation from other birds. Nests were flared-rim cups, fashioned of mud or guano pellets, and usually attached high on walls or in pockets eroded in the cave ceiling.

Sample culverts were of multiple-passageway concrete construction and were selected from a series of 16 culverts that averaged 1.6 km apart. The series averaged ca. 17 breeding pairs of swallows (*P. fulva* and *H. rustica*) per culvert; culverts with greater concentrations of swallows usually were separated by culverts possessing considerably fewer birds; no culvert held over 80 breeding pairs. The four sample culverts held from 6–32 nesting pairs of *P. fulva*; *H. rustica* formed 49% of the overall total of breeding swallows in these culverts. Culverts 54, 51, 48 and 40 had 6, 5, 11 and 10 passages, respectively, that averaged 15.1 m × 1.6 m × 1.7 m (length × width × height). Nests of both *P. fulva* and *H. rustica* usually were built on culvert walls within 0.3 m of their ceilings.

Nests were identified individually by inserting numbered nails into nest bases or by marking adjacent surfaces with pencil. Active nests accessible by ladder formed the annual samples at Dunbar Cave; approximately 40% of the nests of the colony were marked. During 1974, nest contents usually were examined at 2- to 3-day intervals; a total of 35 visits was made to the cave (Fig. 1). Fifty-two visits were made to the site in 1975. Early in the 1975 season, during three periods of 6, 10 and 9 days (Fig. 1), nest contents were examined daily to determine incubation and nestling periods; before and between these periods of daily visitation and after 8 June 1975, the 1975 visitation schedule approximated that of 1974. Culverts were visited in 1974 on the same days as cave visits.

Since *P. fulva* lay on successive days until clutch completion, clutch initiation dates not

APRIL   MAY   JUNE

1974 |‖‖‖‖‖‖‖|‖‖‖‖‖ ‖ ‖‖‖ ‖‖‖|‖‖‖‖‖‖ ‖‖‖‖‖ ‖‖‖‖ ‖‖ ‖‖‖ ‖‖|‖ ‖‖‖‖‖ ‖‖ ‖‖‖ ‖‖ ‖‖‖ ‖‖|

1975 |‖‖‖‖‖‖‖‖‖‖‖‖‖ ‖‖ ‖‖‖ ‖‖ ▮▮▮▮ ‖ ‖‖‖ ▮▮▮▮▮▮ ‖‖ ‖‖ ‖‖‖ ‖‖‖ ▮▮▮▮ ‖ ‖‖‖‖ ‖‖ ‖‖‖ ‖‖‖ ‖‖‖
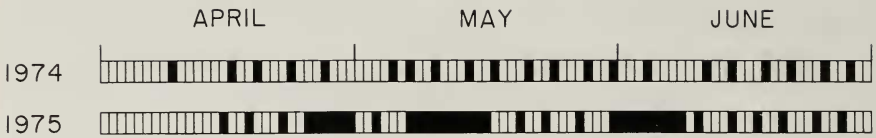
Fig. 1. Investigator nest-visitation schedules at Dunbar Cave during the first reproductive cycle of 1974 and of 1975. Small black rectangles represent dates on which nests were visited by the investigator; small vacant rectangles, dates on which nests were not visited.

known precisely were determined by backdating from the sampling day on which eggs first were found in the nest; similarly, clutch completion dates were determined by forward dating to account for all eggs observed. When hatch time was not known exactly, the average incubation period of 15 days (Martin et al. 1977) was substituted. Due to our sampling schedule, "hatch" data may include very early nestling mortality (Martin et al. 1977). Egg loss and nestling mortality to 19 days post-hatch (1 day prior to flight potential) arbitrarily were assigned to the midpoints of the sampling gaps during which they occurred.

Due to the more intensive (daily) visitation program in early 1975, more precise hatch and survival data were available for nests examined during this period than for those visited at other times. These daily data were not used in scoring of reproductive events reported here; for this purpose, only data gathered on visits of a predetermined schedule that approximated the regular (2–3-day interval) schedule were used (Fig. 1). Except for comparisons of correlation coefficients, or where noted otherwise, statistical comparisons employed the Mann-Whitney U-test (Sokal and Rohlf 1969). Results of statistical tests were considered significant at $P < 0.05$.

RESULTS

Environmental variables.—Precipitation data for periods preceding and during the 1974 and 1975 reproductive seasons of the cave population and the 1974 reproductive season of the culvert populations are presented in Table 1. Precipitation in the area of Dunbar Cave was considerably greater in 1975 than in 1974. Precipitation at the culvert area was only slightly higher than at Dunbar Cave in 1974. Breeding season (April–August) mean temperatures at the area surrounding Dunbar Cave were similar in 1974 (25.6°C) and 1975 (24.3°C). Temperature records for the culvert area are incomplete for June 1974, but the cumulative mean for the remaining months of the breeding season approximates that for the cave area (cave–25.1°C; culverts–24.4°C) in 1974. The thermal regime at cave nests during the breeding season (17–22°C, season minima and maxima; 3°C maximum daily fluctuation) was less variable than that at a sample culvert (14–32°C, season minima and maxima; 8°C maximum daily fluctuation). A moist substrate of mud and guano provided a constantly available source of nesting material to the cave colony, while culvert-nesting birds frequently travelled longer distances to gather mud. The potential of catastrophic loss due to flooding existed for culvert, but not cave populations.

The cave population also was exposed to fewer biotic variables. No other swallows nested near Dunbar Cave, while culvert *P. fulva* nested syntopically with nearly equal numbers (49%, 1974) of Barn Swallows. Vertebrate nest predators were not seen at Dunbar Cave, nor is it likely that they could pose a serious threat at such a site. Eggs and nestlings in culverts were exposed to attack or predation by at least six species of mammals, two species of birds and six species of snakes, in addition to ants and several other invertebrates (Martin, unpubl.). Casual human disturbance is minimal at Dunbar Cave because the cavern is non-commercial, lies on private property and entry is difficult without specialized equipment. Culvert colonies, however, are disturbed regularly by itinerants and highway maintenance crews. Although catastrophic losses due to deliberate human perturbation occur occasionally in culverts, none occurred in sample culverts in 1974.

Reproduction at Dunbar Cave.—Clutch-size ranged from 1–6 eggs. Clutches of 3–5 eggs comprised 96.3% of all clutches (Tables 2, 3) and clutches of one, two and six eggs comrpised, respectively, 0.9%, 2.6% and 0.2% of all clutches. Clutches were divided arbitrarily into early and late categories according to waves of synchrony in laying. Comparative distributive statistics for clutch-size, hatch (no. of young hatched) and survival (no. of young surviving to 19 days) of these and total first and later clutches of 1974 and 1975 are presented in Table 2. Overall percentage values of hatched young/eggs laid, surviving nestlings/hatched young, and surviving nestlings/eggs laid, also are presented in Table 2. Table 4 depicts a matrix of results of statistical testing relating fecundity and reproductive success to precipitation in the study area.

Clutch-size, hatch and survival decreased with time within and between clutch categories in 1974 (Tables 2, 4); these decreases were statistically significant (Table 4). In 1975, clutch-size decreased significantly within and between clutch categories (Table 4). Although hatch and survival in 1975 decreased between early and late first clutches, these decreases were not statistically significant (Table 4). Hatch and survival decreased significantly between early and late second clutches in 1975 (Table 4). No significant differences in hatch and survival occurred between first and second clutches in 1975.

To assess the effects of differential perturbation, comparisons of data for 56 nests in which contents (eggs and nestlings) were marked and 70 in which contents were unmarked were made for first clutches of 1975. Hatch was not significantly lower in nests with marked eggs (2.71 ± 0.20, marked vs 3.00 ± 0.16, unmarked; $0.1 > P > 0.05$, NS). Survival was significantly lower in nests with marked contents (2.43 ± 0.18, marked vs 2.84 ± 0.15, unmarked; $P < 0.05$). Comparisons of hatch percentage and survival/hatch percentage indicated that the former was 17% lower in nests with

TABLE 2

REPRODUCTIVE STATISTICS AND HATCH-SURVIVAL PERCENTAGES FOR NESTS OF *P. FULVA*
AT DUNBAR CAVE (1974 AND 1975) AND CULVERT SITES (1974)

Clutch sequence[1]	N	Clutch-size $\bar{x} \pm SE$	Young hatched $\bar{x} \pm SE$	Survival (19 days) $\bar{x} \pm SE$	Hatch/ laid	Survive/ hatch	Survive/ laid
Cave 1974							
Clutch 1 early (before 11 May)	87	3.95 ± 0.069	3.26 ± 0.133	2.78 ± 0.145	0.82	0.85	0.70
Clutch 1 late (11 May– 1 July)	28	3.61 ± 0.129	2.86 ± 0.250	1.75 ± 0.227	0.79	0.61	0.49
Clutch 2 early (before 30 June)	65	3.45 ± 0.102	2.55 ± 0.140	1.31 ± 0.141	0.74	0.51	0.38
Clutch 2 late (July)	8	2.75 ± 0.163	1.00 ± 0.499	0.63 ± 0.419	0.36	0.63	0.23
Total clutch 1	115	3.87 ± 0.062	3.17 ± 0.118	2.53 ± 0.129	0.81	0.80	0.65
Total clutch 2	73	3.37 ± 0.096	2.40 ± 0.146	1.22 ± 0.136	0.71	0.52	0.37
Total (1 + 2)	188				0.78	0.71	0.54
Cave 1975							
Clutch 1 early (before 11 May)	111	4.03 ± 0.057	2.93 ± 0.128	2.67 ± 0.125	0.73	0.91	0.66
Clutch 1 late (11 May– 1 July)	15	3.47 ± 0.133	2.47 ± 0.412	2.33 ± 0.398	0.71	0.95	0.67
Clutch 2 early (before 30 June)	99	3.71 ± 0.052	3.18 ± 0.105	2.81 ± 0.125	0.86	0.88	0.76
Clutch 2 late (July)	8	2.88 ± 0.294	2.38 ± 0.323	2.13 ± 0.295	0.83	0.89	0.74
Total clutch 1	126	3.96 ± 0.055	2.87 ± 0.123	2.63 ± 0.120	0.73	0.91	0.66
Total clutch 2	107	3.64 ± 0.056	3.12 ± 0.102	2.76 ± 0.119	0.86	0.88	0.76
Total clutch 3	8	3.13 ± 0.124	2.00 ± 0.597	2.00 ± 0.597	0.64	1.00	0.64
Total (1 + 2 + 3)	241				0.78	0.90	0.70
Culverts 1974							
Total clutch 1	81	4.31 ± 0.065	3.44 ± 0.119	3.25 ± 0.127	0.79	0.94	0.75
Total clutch 2	49	3.96 ± 0.087	3.22 ± 0.166	2.92 ± 0.184	0.81	0.90	0.74
Total clutch 3	8	3.50 ± 0.188	2.38 ± 0.564	1.63 ± 0.497	0.68	0.16	0.11
Total (1 + 2 + 3)	138				0.79	0.90	0.72

[1] Chronology by nest, not adult pair; adults unmarked.

TABLE 3
NESTLING SURVIVAL (TO 19 DAYS) IN RELATION TO MOST COMMON CLUTCH-SIZES IN
P. FULVA

	Clutch-size	Frequency	% nestlings surviving	Nestling survival per brood ($\bar{x}$)
Cave (1974)				
Clutch 1	3	22	70	2.10
	4	76	65	2.60
	5	14	63	3.15
Clutch 2	3	34	42	1.26
	4	31	35	1.39
Cave (1975)				
Clutch 1	3	24	74	2.22
	4	80	65	2.60
	5	21	66	3.30
Clutch 2	3	29	76	2.28
	4	72	76	3.05
Culvert (1974)				
Clutch 1	3	5	87	2.61
	4	46	84	3.36
	5	30	64	3.20
Clutch 2	3	10	67	2.00
	4	31	75	3.00

marked contents (63% vs 80%), while the latter was only 1% lower (91% vs 92%).

No significant differences in clutch-size, hatch and survival existed between 1974 and 1975 first clutches (early, late and total). However, second-clutch size, hatch and survival increased from 1974–1975; with one exception (size of late second clutch), these differences were statistically significant (Table 4).

When cumulative reproductive data for both clutches of 1974 and 1975 were compared (Table 2; total 1 + 2 vs total 1 + 2 + 3), hatch percentages were equal, but nestling survival percentages were considerably higher in 1975. These differences were due primarily to very high nestling survival within the second brood of 1975 (Table 2).

Mean nestling survival per brood increased with clutch-size in both clutches of both study years at Dunbar Cave (Table 3); three of four correlation coefficients calculated for Dunbar Cave clutches indicated a moderate, but significant positive correlation between them (Table 5).

TABLE 4

STATISTICAL COMPARISONS AMONG SAMPLES REPRESENTED BY CLUTCH-SIZE, HATCH AND SURVIVAL MEANS FOR 1974 AND 1975 *P. FULVA* CLUTCHES AT DUNBAR CAVE[1]

	Clutch-size			Hatch			Survive		
	1974 Dry		1975 Wet	1974 Dry		1975 Wet	1974 Dry		1975 Wet
Clutch 1									
Early	3.95	NS	4.03+	3.26	NS	2.93+	2.78	NS	2.67+
	*		***	*		NS	***		NS
Late	3.61	NS	3.47+	2.86	NS	2.47+	1.75	NS	2.33+
Clutch 2									
Early	3.45	**	3.71	2.55	***	3.18	1.31	***	2.81
	**		**	**		**	*		*
Late	2.75	NS	2.88	1.00	*	2.38	0.63	*	2.13
Total clutches									
1	3.87	NS	3.96+	3.17	NS	2.87+	2.53	NS	2.63+
	***		***	***		NS	***		NS
2	3.37	**	3.64	2.40	***	3.12	1.22	***	2.76
			**			*			NS
3			3.13			2.00			2.00

[1] Asterisks appear (vertically and horizontally) between means representing samples between which statistically significant 1-tailed Mann-Whitney *U*-tests were performed (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. NS = results not significant. Hypothesis tested: fecundity and reproductive success are directly related to amount of precipitation in xeric areas.
+ follows data for nests periodically under daily observation.

The number of nests in the sample area increased approximately 10% from 1974–1975 (Tables 2, 6). Sixty-three percent of nests that held an early clutch in 1974 received a second clutch, while 84% of the 1975 nests were laid in a second time (Tables 2, 6). Largely due to increased second-clutch size and nestling survival, 261 more young survived to 19 days in

TABLE 5

RELATIONSHIPS (REGRESSION EQUATIONS AND CORRELATION COEFFICIENTS) BETWEEN NESTLING SURVIVAL (Y) AND CLUTCH-SIZE (X)

		Clutch 1		Clutch 2	
Location	Year	Regression equation	*r*	Regression equation	*r*
Cave	1974	Y = −0.043 + 0.663X	0.318**[1]	Y = 0.329 + 0.272X	0.192
Cave	1975	Y = 0.263 + 0.597X	0.276**	Y = −0.514 + 0.898X	0.426***
Culvert	1974	Y = 2.950 + 0.067X	0.034	Y = −0.359 + 0.828X	0.392**

[1] Asterisks follow correlation coefficients that are statistically significant (** $P < 0.01$; *** $P < 0.001$).

TABLE 6
NUMBERS OF NESTLINGS SURVIVING TO 19 DAYS AT CAVE AND CULVERT STUDY SITES

| | Dunbar Cave | | | | Culvert sites | |
| | 1974 | | 1975 | | 1974 | |
	# Young	# Nests	# Young	# Nests	# Young	# Nests
Clutch 1	290	115	331	126	263	81
Clutch 2	91	73	295	107	143	49
Clutch 3	—	—	16	8	13	8
Total	381		642		419	

the sampled area in 1975 than in 1974, an increase in survival of 40% (Table 6).

Reproduction at culvert sites.—Clutch-size for 1974 culvert-nesting *P. fulva* ranged from 3–5 (Table 3). Distributive statistics for grouped culvert-site reproductive data are shown in Table 2. Since separate culverts were involved, overall nesting synchrony was reduced (see, also, Myres 1957) and chronological (early–late) dichotomies could not be assigned within clutches. As in cave-nesting *P. fulva*, clutch-size, hatch and survival decreased in culvert birds from first to second clutches (Table 2); of these decreases, only that between clutch-size of clutches one and two was statistically significant ($P < 0.005$). Reproductive parameters declined further in the few third clutches deposited. Hatch and survival percentages of first and second clutches were similar (Table 2).

Mean nestling survival per brood increased from clutches of three to clutches of four for the first clutch, but decreased slightly for clutches of five (Table 3); the correlation coefficient for these variates was not significant (Table 5). Mean nestling survival per brood increased with clutch-size in the second clutch (Table 3); the correlation coefficient for these variates was statistically significant (Table 5).

Comparisons between cave and culvert populations.—Clutch-size, hatch and nestling survival of first and second clutches were higher for the culvert populations than for the cave colony in 1974 (Table 2); with one exception (first clutch hatch $0.1 > P > 0.05$, NS), these differences were highly significant ($P < 0.001$). In 1974, a third clutch was deposited in some culvert nests, but in no cave nests (Table 2). Overall (total) hatch percentages were similar at culvert and cave in 1974, but total survival

percentages were considerably higher at culvert colonies (Table 2). At the culvert sites, approximately 30% fewer nests produced a total of about 10% more surviving nestlings (Tables 2, 6); much of this difference was due to high second clutch reproductive success.

<div align="center">DISCUSSION</div>

Pattern of food availability generally is considered a major determinant of variation in avian reproduction (Lack 1954; Klomp 1970; Cody 1971; Ricklefs 1969, 1973; von Haartman 1971; Dingle and Khamala 1972; Immelmann 1973; Bryant 1975). Other environmental factors, in turn, influence food availability and also may affect reproduction in other ways. Much information relating reproductive parameters of birds to precipitation has developed in the past few decades; in arid regions, reproductive timing and success appear particularly closely tied to the pattern of rainfall (for example, Moreau 1944; Lack 1954; Keast and Marshall 1954; Immelmann 1963, 1973; Dingle and Khamala 1972; Sinclair 1978). Amount of rainfall frequently appears to influence reproduction through food chain effects but also may affect reproduction indirectly if the availability of nesting material and nest concealment are altered. Although Cave Swallows are constrained in nest building by scarcity of mud in some areas (Baker 1962), neither this moisture-dependent limitation, nor that of nest concealment by foliage are operative at Dunbar Cave (although the former may be a factor at culvert sites), and it is assumed that moisture-related constraints, if operative here, influence reproduction primarily through limitation of food resources.

Seasonal variation in reproductive parameters.—The seasonal decrease in clutch-size exhibited by *P. fulva* is typical of some populations of Cliff Swallow (*P. phrrhonota*) and *H. rustica,* swallows with which it nests syntopically (Samuel 1971, Graber et al. 1972, Anthony and Ely 1976, Grant and Quay 1977), as well as other passerines (Lack 1954, Klomp 1970, von Haartman 1971, other reviews). In *P. fulva,* hatch and nestling survival usually decline seasonally also (Tables 2, 4; Martin, unpubl.); these declines are particularly evident when the perturbed first clutch of 1975 is excluded from comparisons. The effect of day length on foraging time and that of prevailing regional precipitation pattern on food resources may determine seasonal (between-clutch) differences in avian fecundity (Lack 1954, Klomp 1970). Day length does not appear to be an important factor at the present study areas, however, for maximum day length occurs here just past the midpoint of the period including the first and second reproductive cycles. A stronger argument may be made for precipitation as an indirect determinant of seasonal productivity of *P. fulva.* In this region, a bimodal annual pattern of rainfall exists, with maxima occurring during April, May

TABLE 7

SEASONAL PRECIPITATION AND TEMPERATURE PATTERNS FOR REGION INCLUDING STUDY
AREAS (35 YEAR AVERAGES)

Month	Mean monthly precipitation (cm)	Mean monthly maximum temperature (°C)
Jan.	2.36	16.4
Feb.	2.92	18.9
Mar.	2.29	22.9
Apr.	5.88	28.3
May	7.37	30.8
June	7.54	33.2
July	3.84	36.2
Aug.	4.72	35.9
Sept.	7.59	32.6
Oct.	5.33	27.3
Nov.	2.06	21.9
Dec.	2.29	17.7

and June, and again in September and October (Table 7; NOAA 1975,
1976). During the breeding season, precipitation usually is lowest during
July and early August, during the second reproductive cycle. In addition,
temperature is maximal during this period (NOAA 1974, 1976), and con-
tributes to moisture deficiency through evaporation.

Annual variation in reproductive parameters.—At Dunbar Cave, a great-
er number of second clutches, in concert with increased clutch-size, hatch
and survival within second clutches, contributed to make the wet repro-
ductive season of 1975 considerably more productive than the relatively
dry season of 1974 (Tables 1, 2, 4, 6). Similar patterns of high fecundity
during years of high rainfall and abundant food resources (Hoesch 1936,
Guirtchitch 1937, Moreau 1944, Lack 1954) or of dependence of repro-
duction on precipitation (Keast and Marshall 1954, Immelmann 1963, Col-
lias and Collias 1978, Sinclair 1978) have been well documented in arid
regions.

First clutch reproductive parameters of the Dunbar Cave colony did not
increase markedly from 1974–1975. This was not unexpected, considering
the increased perturbation to which individual nests and the entire colony
were subjected during the first reproductive cycle of 1975 (Methods, also
Fig. 1). Data taken under perturbed conditions may be of somewhat limited
value for comparative purposes, but the environment of much of the North
Temperate Zone is heavily disturbed (Lack 1965), and data reflecting quan-

titatively the potential effects of methodology are relevant. The lower survival in nests whose contents were marked appeared to be due largely to low hatchability. Losses ascribed to desertion occurred at approximately equal frequency in both marked (10%) and unmarked (11%) samples. These intra-clutch data represent only the proximal individual effects of marking and must be considered together with the more widespread and concomitant effects expected from disturbance of the entire colony: potential impairment of synchrony and attentiveness, and disruption of nestling and adult feeding patterns.

Comparisons between cave and culvert populations (1974).—Disturbance by humans is not a normal phenomenon at Dunbar Cave, but colonies of *P. fulva* that nest in highway culverts have undergone regular anthropogenic disturbance and risk and are subjected to other catastrophic and non-catastrophic biological and physical influences to which the cave colony is not exposed. Populations evolving in variable environments often display greater reproductive effort than those adapted to more stable conditions; theoretically, this increased effort balances increased mortality (Cody 1966, 1971). First and second clutches were larger in culvert populations than at Dunbar Cave and third clutches occurred only at culvert sites in 1974. Hatch and nestling survival of first and second clutches were higher in culverts as were overall hatching and survival percentages, the greatest difference appearing in comparisons between second clutches. Following Cody's postulations (1966, 1971), an ultimate interpretation of the data would be that differential mortality between culvert and cave populations (culvert mortality > cave) must occur at or after fledging. I believe that this is probable; recently fledged *P. fulva* usually remain in the vicinity of the culvert and return to the nest for several days, and, lacking in-flight strength and maneuverability, are exposed heavily to the hazard of vehicle strike. Relevant to the evaluation of this interpretation are the estimated maximal chronological separation of culvert from cave populations (20 generations) and the distance between them (65–80 km).

Density-dependent effects may be involved in the higher fecundity, hatch and nestling survival of culvert-nesting *P. fulva*; in other species such relationships are well documented for clutch-size, less adequately so for nestling survival (Klomp 1970, von Haartman 1971). Culvert nesting has been established only recently in central Texas, and has resulted in marked range expansion (Martin and Martin 1978). Although the culverts sampled in this study are not at the current edge of the range of *P. fulva*, their swallow densities (both conspecific and cumulative) are lower than at Dunbar Cave.

SUMMARY

Data on reproduction from Texas cave and culvert sites are presented for the Cave Swallow (*Petrochelidon fulva*), a peripheral U.S. species presently undergoing breakdown in ecological segregation at the northern margin of its range through modification of its nesting habits. Correlations exist between environmental influences, both natural and anthropogenic, and variation in pattern of reproduction of cave- and culvert-nesting colonies of this species. Seasonal declines in reproductive parameters occurred at both sites and are considered to reflect adaptations to within-season increasing aridity and diminished food supply. During a relatively wet year at a cavern-nesting colony, overall seasonal reproductive output and nestling survival were higher than during a drier year; much of this difference was due to significantly increased second clutch reproductive parameters. Increased investigator visitation of the cave colony during the first reproductive cycle of the wet year may have negatively affected hatch and survival of that year's first clutch. Culvert-nesting populations displayed significantly higher clutch-size and nestling survival than did the population nesting at the more typical cave site.

ACKNOWLEDGMENTS

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